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NOTES FOR STUDENTS

Graft hybrids and chimeras.—The large amount of recent work on graft hybrids, which has resulted in such astonishing discoveries as to their exact nature, seems to call for a collective review. In 1825 M. ADAM, a French horticulturist, by grafting *Cytisus purpureus* (a small tufted species) on *Laburnum vulgare* (an arborescent species) was much surprised to find that there resulted a shoot with somewhat intermediate characters. While the original individual has long been dead, the new form has been propagated by grafting and is somewhat common in cultivation; to it there has been given the name *Laburnum Adami*, and generally it has been regarded as a graft hybrid. Scarcely second in reputation to this, the most famous of the "graft hybrids," is *Crataegomespilus*, which is supposed to be a graft hybrid between *Crataegus monogyna* and *Mespilus germanica*; in this case the original tree is said still to exist in Lorraine. A third supposed case of a graft hybrid is the Bizzaria orange, which is thought to have arisen through the intergrafting of *Citrus Aurantium* and *C. medica*. While much study has been made of these peculiar plant forms, it is only very recently that their nature has been understood.

The present phase of graft hybrid investigation dates from a paper by HANS WINKLER, published in 1907.³ Although the results of this first paper were somewhat disappointing, they deserve mention, because they opened up a new method of investigation. A scion of *Solanum nigrum* was grafted on *S. Lycopersicum*, and after growth had been resumed, a transverse cut was made in such a way as to sever both stock and scion, it being hoped that adventive shoots would grow from the cut surface along the line of contact of stock and scion. Such adventive shoots actually appeared, and in one case the new shoot involved tissues of both stock and scion. However, the new form was not a graft hybrid, for clearly one side of the shoot was *Solanum nigrum* and the other *S. Lycopersicum*; to this peculiar structure WINKLER gave the suggestive name *chimera*. So sharply marked was the line between the tomato and the nightshade that some leaves were partly of one species and partly of the other. WINKLER's method soon yielded the results he had been seeking, for in 1908 he announced the production of a true graft hybrid,⁴ a notable result, since never before had this been done under exact experimental control. To the new form there was given the name *Solanum tubingense*, in honor of the university town where the plant was produced. Out of 268 grafts between the tomato and the nightshade, there arose over 3000 adventitious shoots, among which there were five chimeras and the supposed graft hybrid *Solanum tubingense*; the latter, while intermediate in character, is somewhat closer to the nightshade than to the tomato. Early in 1909 WINKLER reported

³ WINKLER, HANS, Ueber Propfbastarde und pflanzliche Chimären. Ber. Deutsch. Bot. Gesell. 25:568-576. figs. 3. 1907; see BOT. GAZETTE 47:84. 1909.

⁴ ———, *Solanum tubingense*, ein echter Propfbastard zwischen Tomate und Nachtschatten. Ber. Deutsch. Bot. Gesell. 26a:595-608. figs. 2. 1908; see BOT. GAZETTE 47:250. 1909.

the production of several more "graft hybrids" by the use of the same methods.⁵ In this paper four varieties of graft hybrids are described, and are given the names *Solanum Darwinianum*, *S. Gaertnerianum*, *S. proteus*, and *S. Koelreuterianum*; the first two resemble the nightshade more than the tomato, while the last two are closer to the tomato. Some of the new forms appeared more than once in the cultures, *S. Gaertnerianum*, for example, being observed to arise five times. Some of the new forms appeared as branches from chimeras. In a recent paper⁶ WINKLER reports the results of a study of the progeny of the new forms. Although the vegetative shoots seem able to fuse and merge readily in various ways, the tomato and nightshade cannot be hybridized sexually. WINKLER observes that the "graft hybrids" without exception revert to the nearer parent, the seedlings of *Solanum tubigense*, *S. Darwinianum*, and *S. Gaertnerianum* always being *S. nigrum*, while the seedlings of *S. proteus* and *S. Koelreuterianum* always are *S. Lycopersicum*. The new forms may be hybridized sexually with the nearest parent form, the progeny being pure nightshade or tomato, as the case may be. Furthermore, reversion in the vegetative shoots is to the nearer parent form.

While WINKLER's results are accepted without debate, his interpretation has been called in question by various investigators. It may be noted that the behavior of the new *Solanum* forms is altogether like that of *Laburnum Adami*, which often shows vegetative reversion to one of the parent forms, and whose seeds give rise not to *L. Adami*, but to *L. vulgare*. STRASBURGER, who always has consistently opposed the reality of graft hybrids on cytological grounds, has taken up the new *Solanum* forms, calling them *hyperchimeras*, that is, more or less complicated chimeras, in which the elements of the two parent forms are more or less intermingled but without any real nuclear fusion (see below).⁷ Of much greater significance are some recent investigations by ERWIN BAUR, and his results bid fair not only to cause a different interpretation to be placed upon WINKLER's results than has been made by either WINKLER or STRASBURGER, but to revolutionize our notions along certain lines as to the possibilities of plants. BAUR has found from a careful study of geraniums with white-margined leaves⁸ that the green cells and colorless cells each are descended from others of their kind, the peripheral portions (composing two or three rows) being colorless (though containing chromatophores) and the internal portions green, and the limits between them being

⁵ WINKLER, HANS, Weitere Mitteilungen über Propfbastarde. Zeitschr. Bot. 1:315-345. pl. 1. figs. 4. 1909; see BOT. GAZETTE 48:478. 1909.

⁶ ———, Ueber die Nachkommenschaft der *Solanum*-Propfbastarde und die Chromosomenzahlen ihrer Keimzellen. Zeitschr. Bot. 2:1-38. 1910; see BOT. GAZETTE 49:386. 1910.

⁷ STRASBURGER, EDUARD, Meine Stellungnahme zur Frage der Propfbastarde. Ber. Deutsch. Bot. Gesell. 27:511-528. 1909.

⁸ BAUR, ERWIN, Das Wesen und die Erbliehkeitsverhältnisse der "Varietates albomarginatae Hort." von *Pelargonium zonale*. Zeit. Abst. Vererbungslehre 1:330-351. figs. 20. 1909; see BOT. GAZETTE 48:72. 1909.

sharp. Since the sexual cells are from the peripheral white portion, the seedlings give pure white forms. White branches give only white forms vegetatively, and green branches only green forms. If a pure white and a pure green form are hybridized sexually, there result, besides pure white and pure green offspring, green-white mosaics. If in the latter the growing point is situated on the line between the white and green portions, there results a chimera, such as WINKLER obtained so frequently in *Solanum*. Since in a cross-section of a stem the two components appear as sectors, BAUR has given to such forms the name *sectorial chimeras*. For the condition that BAUR finds in an ordinary *Pelargonium* with white-margined leaves, he gives the name *periclinal chimeras*, one of the components investing the other; in *Pelargonium* the growing point is periclinally divided into white and green cells, the former outermost, so that the entire plant is composed of a body of green geranium invested by a mantle, two or three cells deep, of white geranium. In referring to WINKLER's work, BAUR suggested that the so-called graft hybrids of *Solanum* probably are periclinal chimeras. In another paper⁹ he discusses STRASBURGER's theories concerning hyperchimeras, noting that such an irregular mixture of the elements of the two component forms can hardly give rise to such definite structures as the so-called graft hybrids. Very recently BAUR has published a résumé of his work on *Pelargonium*, and on the graft hybrid question generally.¹⁰ He has discovered also that *Crataegomespilus* is a periclinal chimera, the form known as *C. Asnieresii* being composed of a *Crataegus* body with a *Mespilus* epidermis; while the form known as *C. Dardari* has a *Mespilus* periphery of two cell layers. *Laburnum Adami*, which has been a riddle for nearly a century, proves to be a periclinal chimera, with an epidermis of *Cytisus purpureus* and a body of *Laburnum vulgare*; seedlings are always the latter, because the hypodermal layer, which gives rise to the sex cells, is of that species. When the peripheral species is composed of two or more layers, the seedlings are of that species, as in *Pelargonium*. One of the most interesting features of a situation that is throughout of absorbing interest is that BAUR's remarkable discovery was almost made by MACFARLANE¹¹ fifteen years ago, as BAUR himself points out. MACFARLANE made a careful anatomical study of *Laburnum Adami* in comparison with *Cytisus purpureus* and *Laburnum vulgare*, and an examination of his figures shows clearly that *Laburnum Adami* agrees with *Cytisus purpureus* as to its epidermis, and with *Laburnum vulgare* as to its body. Indeed MACFARLANE says: "The very striking resemblance which the epidermis of the hybrid portion has to that of *C. purpureus* . . . would seem at first sight to prove that

⁹ BAUR, ERWIN, Propfbastarde, Periklinalchimären, und Hyperchimären. Ber. Deutsch. Bot. Gesell. 27:603-605. 1910.

¹⁰ ———, Propfbastarde. Biol. Centralbl. 30:497-514. figs. 7. 1910.

¹¹ MACFARLANE, J. M., A comparison of the minute structure of plant hybrids with that of their parents, and its bearing on biological problems. Trans. Roy. Soc. Edinburgh 37:203-286. 1895.

the hybrid portion was wrapped around, so to speak, by an epidermis of *C. purpureus*.” Very recently BUDER has reinvestigated *Laburnum Adami*,¹² and has brought additional evidence to show that BAUR’s view is correct. Finally, WINKLER, in his latest paper,¹³ states that a study of his *Solanum* forms from BAUR’s viewpoint discloses that for the most part they are, as BAUR thought likely, periclinal chimeras. Here he suggests that what have been taken to be graft hybrids may (theoretically) be actual graft hybrids, resulting from the fusion of the somatic cells of different species; or again they may have a hybrid nature, owing to the migration between stock and scion of various substances (as atropin or nicotin in the Solanaceae); or finally they may be chimeras, where the possibility lies open that they may be hyperchimeras, sectorial chimeras, or periclinal chimeras. Careful cytological study has shown that *Solanum tubingense*, *S. proteus*, *S. Koelreuterianum*, and *S. Gaertnerianum* are periclinal chimeras. *S. tubingense* has a nightshade body and a tomato epidermis; *S. Koelreuterianum* has the reverse relation of the two components; *S. proteus* has a tomato periphery of two cell layers, and it is probable that *S. Gaertnerianum* has the reverse relation. WINKLER thinks, however, and the cytological evidence noted is confirmatory, that in *Solanum Darwinianum* he has a true graft hybrid that was produced by the fusion of vegetative cells of the nightshade and tomato. If this is proven to be correct, it will stand, not only as the first experimentally produced graft hybrid, but as the only certain instance on record of such a form. The discoveries of WINKLER and BAUR open a new path in experimental biology, and to one as much as to the other belongs the credit that goes to the pioneer; to WINKLER, because his brilliant work has made possible the experimental study of these problems, and because his studies mark the opening of a new line of investigation; to BAUR, because he has solved the riddle of nearly a century, and because he has made possible the interpretation of WINKLER’s results. It goes without saying that biologists will wait with eager expectancy the announcement of new results, and that many experimenters will be attracted to the new field.—HENRY C. COWLES.

The cytological aspect of graft hybrids and chimeras may be summarized as follows:

In 1905 and 1907, in papers dealing with the rôle of the chromosome in heredity, STRASBURGER¹⁴ included an account of his investigations upon

¹² BUDER, JOHANNES, Studien an *Laburnum Adami*. Ber. Deutsch. Bot. Gesell. **28**:188–192. 1910.

¹³ WINKLER, HANS, Ueber das Wesen der Propfbastarde. Ber. Deutsch. Bot. Gesell. **28**:116–118. 1910.

¹⁴ STRASBURGER, E., Histologische Beiträge zur Vererbungsfrage. I. Typische und allotypische Kernteilung. Jahrb. Wiss. Bot. **42**:1–70. pl. 1. 1905.

———, Ueber die Individualität der Chromosomen und die Propfhybriden-Frage. Op. cit. **44**:482–555. pls. 5–8. 1907.

Laburnum Adami. If this plant is really a hybrid, owing its origin to a fusion of diploid nuclei of *Laburnum vulgare* and *Cytisus purpureus*, its nuclei should be tetraploid; but they were found to be only diploid, and STRASBURGER regarded this as evidence against the hybrid character of the graft. After NĚMEC¹⁵ had reported vegetative fusions of nuclei followed by reduction phenomena in chloralized root tips, STRASBURGER repeated the experiments, but could not confirm NĚMEC's results, and therefore concluded that they had no significance so far as *Laburnum Adami* was concerned, and also that in the structure of their nuclei, plants known as graft hybrids show no indication of a hybrid character.

At this stage in the development of the subject, WINKLER¹⁶ secured from *Solanum Lycopersicum* and *S. nigrum* plants which were acknowledged to be graft hybrids, and he asserted that they would necessitate a fundamental revision of our theories in regard to inheritance, and especially in regard to the rôle of the nucleus in heredity. Since the threatened theories were due to STRASBURGER more than to any other botanist, he felt called upon to defend them, and securing material by grafting *Solanum Lycopersicum* and *S. nigrum*, he examined the nuclei, but did not find them to be different from those of other graft hybrids which he had previously investigated. There was no migration of nuclei, no fusion of nuclei of scion and stock, or any regulative reduction processes. He would regard WINKLER's graft hybrids as more or less complicated chimeras and would call them "hyperchimeras."

In many angiosperm parasites (like mistletoe) the relation between parasite and host is very intimate, but there is no mingling of nuclei. In grafting, it seems possible that a bud from the point of union might give rise to a shoot bearing a flower in which an anther might be from the scion and an ovary might be from the stock. Close fertilization might then give rise to a true hybrid, but hyperchimeras, STRASBURGER thinks, would be more likely to produce flowers, the seeds of which would give rise to pure plants of either the scion or stock.

The fact that pollen from his graft hybrids would cause fertilization in *Solanum nigrum* or *S. Lycopersicum*, while neither of these plants can be crossed with the other, WINKLER regards as proof of hybrid character; but STRASBURGER thinks that the pollen was probable pure, and consequently fertilization was to have been expected, but that only *S. nigrum* or *S. Lycopersicum* would result.

STRASBURGER publishes no figures and refrains from giving a detailed account of nuclear phenomena, because WINKLER's full paper has not yet been published; but his examination satisfies him that WINKLER has produced

¹⁵ NĚMEC, B., Ueber die Entwicklung des Chloralhydrats auf die Kern- und Zellteilung. Jahrb. Wiss. Bot. 39:645-730. 1904.

¹⁶ WINKLER, HANS, Weitere Untersuchungen über Propfbastarde. Zeitschr. Bot. 1:315-345. pl. 1. figs. 4. 1909.

nothing which demands any fundamental revision of his theories in regard to the rôle of the nucleus in heredity.

Soon after this paper by STRASBURGER appeared, WINKLER¹⁷ published a description of the generation obtained from the seed of his graft hybrids, and includes an account of the chromosome numbers. In *Solanum Lycopersicum* the x and $2x$ numbers are 12 and 24; while in *S. nigrum* they are 36 and (probably) 72. He suggests that the difference in chromosome numbers may prevent the crossing of these two species, although he recalls that ROSENBERG crossed two species of *Drosera* with 10 and 20 chromosomes in their x generation, and obtained a hybrid with 30 chromosomes as the $2x$ number. If the *Solanum* graft hybrids are due to a fusion of somatic nuclei, they should have $72 + 24$, or 96 chromosomes, unless the fusion should be followed by a regulative reduction, in which case the number should be 48. WINKLER found the x number to be 36 in *Solanum tubingenense*, *S. Darwinianum*, and *S. Gaertnerianum*, and found 12 in *S. proteus* and in *S. Koelreuterianum*, the first three of these, in their pollen formation, reverting to *S. nigrum*, and the other two reverting to *S. Lycopersicum*. The sterility of *S. Koelreuterianum* and *S. Darwinianum* might be due to a difference in chromosome numbers of microspores and megaspores. The microspore number is 12, but the megaspore number remains to be determined. In all five of the graft hybrids the development of the pollen is regular, but it is still to be determined whether the germ cells are pure or hybrid. WINKLER thinks it is more reasonable to suppose that the graft hybrids more closely resembling *S. nigrum* are from *S. nigrum* cells, and that those resembling *S. Lycopersicum* are from cells of that parent, the nuclei being those of one parent or the other, but the cytoplasm being mingled with that of neighboring cells. If such cytoplasm should have so great an influence, it would interfere with the theory that the nucleus is the sole bearer of hereditary characters.

In an addendum to this paper WINKLER severely criticizes STRASBURGER for publishing anything before the cytological details had been made public. STRASBURGER certainly would not have taken part in the matter had it not been that his cytological theories had been attacked. Had some cytological evidence accompanied WINKLER's attack upon theories which STRASBURGER has held and defended almost for a lifetime, any unpleasantness could have been avoided. In this addendum WINKLER states that in September 1907, at the Dresden meeting of the *Deutsche botanische Gesellschaft*, he had suggested that the *Solanum* graft hybrids might be complicated chimeras, a sort of mosaic of the two parents. This suggestion seems to the reviewer to be a good working hypothesis, and if the suggestion is really a fact, an intensive study of the nuclei and cytoplasm of the graft might enable one to recognize, even in vegetative tissues, just what cells have been derived from each parent, while in the reduction divisions the recognition should not be difficult.

¹⁷ WINKLER, HANS, Ueber die Nachkommenschaft der *Solanum*-Propfbastarde und die Chromosomenzahlen ihrer Keimzellen. Zeitschr. Bot. 2:1-38. 1909.

That there is an interchange of material between nucleus and cytoplasm probably all cytologists will admit, although optical evidence is at present very scanty. It seems quite possible that the whole graft hybrid and chimera question, when the cytological evidence is all in, will emphasize rather than weaken the theory that the nucleus is practically the sole bearer of hereditary characters.

In his most recent account of the chromosomes of these forms WINKLER¹⁸ finds that *Solanum tubingense*, *S. proteus*, *S. Koelreuterianum*, and *S. Gaertnerianum* are periclinal hybrids; while *S. Darwinianum*, at least in the subepidermal layer of the stem apex, is a fusion hybrid (*Verschmelzungs-Propfbastard*). The germ cells of this latter form have 48 chromosomes, and since the parents (*S. nigrum* and *S. Lycopersicum*) have 12 and 36 chromosomes as the reduced numbers, WINKLER infers that the subepidermal layer from which the pollen is derived must have 48 chromosomes; and he supposes that a *S. nigrum* cell with 24 chromosomes has fused with a *S. Lycopersicum* cell with 72, giving rise to a nucleus with 96; and that in the progeny of this nucleus the number has become reduced to 48. Another reduction would then give the required 24. This seems too complicated to be correct.

It is evident that cytological investigation of graft hybrids has only just begun. STRASBURGER early recognized the importance of such investigation, and WINKLER's splendid success in securing the grafts has reopened an attractive field for cytological research. The problems are so numerous and the time demanded for reliable results is so great that one man cannot hope to do all the work. Many have tried to find out whether there is a cytological basis for Mendelism. DEVRIES has welcomed cytological investigations of mutation and has generously furnished material for such work. If WINKLER should welcome others into the field, the facts might soon be uncovered; but if others must wait until he has finished, the task is so great and so complicated that, although a young man, he might grow old with the problem still unsolved.—CHARLES J. CHAMBERLAIN.

Plant diseases.—*Cyanospora albicedrae*, a new generic type, is reported on the mountain cedar of Texas by HEALD and WOLF.¹⁹ The fungus is a pyrenomycete of a peculiar type, having its perithecia prostrate, with the short ostecolum curved outward. The perithecia occur singly or in small groups on whitened areas on the trunks and branches. This whitening of the bark is the most characteristic symptom of the infected trees. The fungus is supposed to be a parasite, although its parasitism is not certain. The present paper is limited to a description of the fungus and its effect on the trees.

A new *Macrophoma* (*M. Phoradendri*) on *Phoradendron flavescens* (Pursh)

¹⁸ WINKLER, HANS, Ueber das Wesen der Propfbastarde. (Vorläufige Mitteilung.) Ber. Deutsch. Bot. Gesell. 28: 116-118. 1910.

¹⁹ HEALD, F. D., and WOLF, F. A., The whitening of the mountain cedar, *Sabina sabinoides* (H. B. K.) Small. Mycologia 2: 205-212. pl. 31. figs. 3. 1910.